

Two new pseudosciurids (Rodentia, Mammalia) from the English Late Eocene, and their implications for phylogeny and speciation

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SYNOPSIS. Assemblages formerly referred to *Treposciurus intermedius* and *Suevosciurus palustris*, from the Solent Group (Late Eocene) of Hordle and of localities in the Isle of Wight (Hampshire Basin), are shown to differ markedly from the type specimens of these species. They are here described as two new species belonging to the original genera. The differences between these two superficially similar species are clarified and evidence for phylogeny and speciation events within the genera is discussed.

INTRODUCTION

Bosma (1974), when describing the rodent faunas of the Isle of Wight Late Eocene and Early Oligocene, attributed two small pseudosciurid species to *Treposciurus intermedius* (Schlosser 1884) and *Suevosciurus palustris* (Misonne 1957). The lectotype of the former is a dentary from the Phosphorites du Quercy of Escamps (old locality), Tarn, southern France, of imprecise but probable Late Eocene age. The holotype of the latter is an upper M¹ or M² from the Sables de Boutersem (Early Oligocene – i.e. immediately post-Grande Coupure) of Hoogbutsel, Belgium. Both type specimens are thus geographically, and in at least one case also stratigraphically, distant from the southern English referred material. They also differ from them in both size and morphology. The *Treposciurus* is rare, but new material from the Hordle Mammal Bed makes it better known.

Abbreviations

The following relate to institutes and/or their specimen numbers. BSPG = Bayerische Staatssammlung für Paläontologie und historische Geologie, München; GIU = Instituut voor Aardwetenschappen, Rijksuniversiteit Utrecht; IRSNB = Institut Royal des Sciences Naturelles de Belgique, Bruxelles; M = register numbers of the Mammal Section, Department of Palaeontology, Natural History Museum, London.

Synonymies

Procedure and terminology follow Matthews (1973).

SYSTEMATIC DESCRIPTIONS

Order **RODENTIA**

Superfamily **THERIDOMYOIDEA**

Family **PSEUDOSCIURIDAE**

Genus **TREPOSCIURUS** Schmidt-Kittler 1970

TYPE SPECIES. *Treposciurus mutabilis* Schmidt-Kittler 1970; Late Eocene, Bavaria, southern Germany.

Treposciurus gardneri sp. nov.

Figs 1–14

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|-----|------|--|
| ?vp | 1973 | <i>Suevosciurus</i> (<i>Microsuevosciurus</i>) aff. <i>minimus</i> (Major 1873); Hartenberger: 16; pl. 1, figs 7–9, 11–13. |
| vp. | 1974 | <i>Treposciurus intermedius</i> (Schlosser 1884); Bosma: 49–52; pl. 6, figs 3–10. |
| vp. | 1974 | <i>Suevosciurus palustris</i> (Misonne 1957); Bosma: pl. 5, fig. 7. |
| v. | 1980 | <i>Treposciurus intermedius</i> (Schlosser 1884); Hooker & Insole: 39. |
| v. | 1982 | <i>Treposciurus intermedius</i> (Schlosser 1884); Russell <i>et al.</i> : 57. |
| v. | 1986 | <i>Treposciurus intermedius</i> (Schlosser 1884); Hooker: 308–311. |
| v. | 1987 | <i>Treposciurus intermedius</i> (Schlosser 1884); Collinson & Hooker: 292. |
| v. | 1987 | <i>Treposciurus</i> sp. nov.; Hooker: 112. |
| v. | 1989 | <i>Treposciurus</i> sp. nov.; Hooker: fig. 2. |

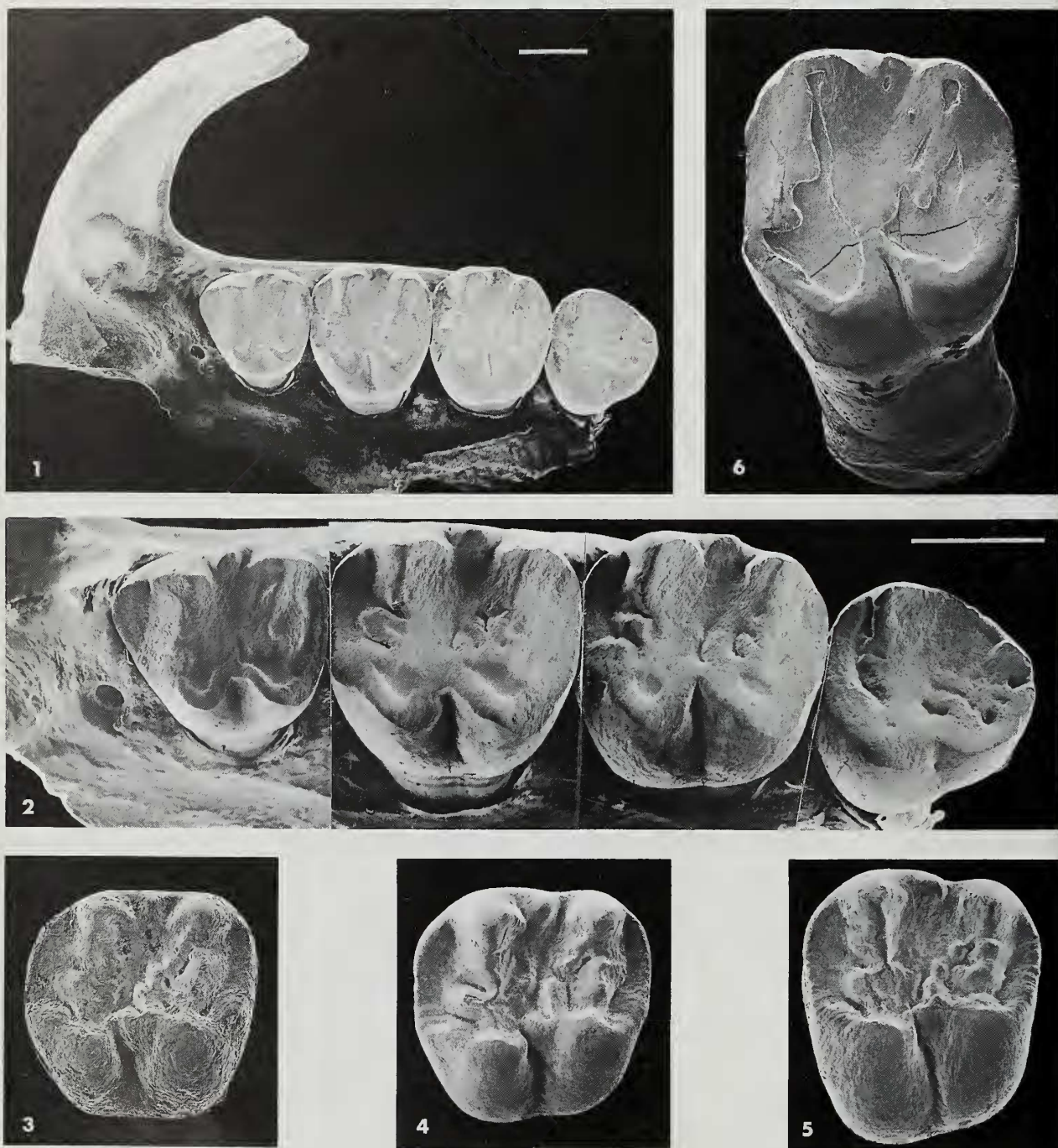
HOLOTYPE. Right maxilla with DP⁴, M¹⁻³ (M44472).

PARATYPES. DP⁴ (M44473), 7 M^{1/2} (M44474–80), 3 DP⁴ (M44481–3), 2 P₄ (M44484–5), right dentary fragment with worn M₁₋₂ (M44486), 9 M_{1/2} (M44487–95), 4 M₃ (M44496–9).

NAME. After Mr R.G. Gardner who collected the type series.

TYPE HORIZON AND LOCALITY. Mammal Bed (see Cray 1973), Totland Bay Member, Headon Hill Formation (see Insole & Daley 1985; previously informally referred to as Lower Headon Beds), Hordle, Hampshire.

REFERRED MATERIAL. Isolated teeth described and figured by Bosma (1974) from sample localities HH1 and HH2, Totland Bay Member; HH3 and other sample localities from 'below the main lignite band', Hatherwood Limestone Member – two M³s and an M_{1/2} from HH3 (GIU 492, 412 and 499) and an M^{1/2} and an M_{1/2} from HH4 (GIU 480 and 426), referred by Bosma to *Suevosciurus palustris* also belong here; all Headon Hill Formation, Headon Hill, Isle of Wight. Also from sample locality WB2A, Bembridge Marls Member, Bouldnor Formation, Whitecliff Bay, Isle of Wight. An M^{1/2} (M51083) from a dark clay at top of limestone overlying *Cyrena cycladiformis* bed (Bristow *et al.* 1889), Totland Bay Member; a DP⁴ (M51084) from shelly lenses at base of lignite bed, Hatherwood Limestone Member (including



Figs 1–6 Scanning electron micrographs (SEMs) of maxilla and upper cheek teeth in occlusal view of *Treposciurus gardneri* sp. nov., Solent Group, late Eocene. Figs 1–5, Mammal Bed, Totland Bay Member, Headon Hill Formation, Hordle, Hants. Figs 1–2, **holotype**, right maxilla, with DP⁴, M^{1–3} and part of zygomatic arch (reversed) (M44472); 2 shows details of the teeth. Figs 3–5, paratype right M^{1/2}s (reversed) (M44474–6). Fig. 6, Bembridge Limestone Formation, Headon Hill, Isle of Wight. Referred right M^{1/2} (reversed) (M51085). Scale bars = 1 mm; specimens uncoated.

sample locality of HH3); isolated upper and lower M1/2s (M44500, M51085-7, M51104) from argillaceous beds within the Bembridge Limestone Formation (including HH6-7 of Bosma, 1974); all Headon Hill; and an M₃ from above a calcareous sandstone, Bembridge Marls Member (level of WB2 of Bosma, 1974), Whitecliff Bay. Probably also the isolated cheek teeth described and figured by Hartenberger (1973) from the upper Calcaire de Fons, Fons 4, Gard, France, as *Suevosciurus* (*Microsuevosciurus*) aff. *minimus*.

DIAGNOSIS. Small species of *Treposciurus* (mean length of M^{1/2} 1.77 mm); cheek teeth with relatively shallow basins, without dense enamel wrinkling or reticulation; upper preultimate molars and DP⁴ with dentine cored (visible only after heavy wear - Fig. 6), interrupted metalophule 1, usually extending buccally to the metacone and joining the endoloph between the hypocone and sinus; lower cheek teeth with weak mesoconid protruding only a short distance into sinusid; lower molars with medium-sized anteroconid, joined to interrupted metalophulid by anterolophulid; M₁₋₂ mesial hypoconid wall more or less vertical, encroaching little on sinusid, which consequently has open appearance; buccal corners of upper molars often noticeably rounded, reflecting lingual retreat of anteroloph and posteroloph.

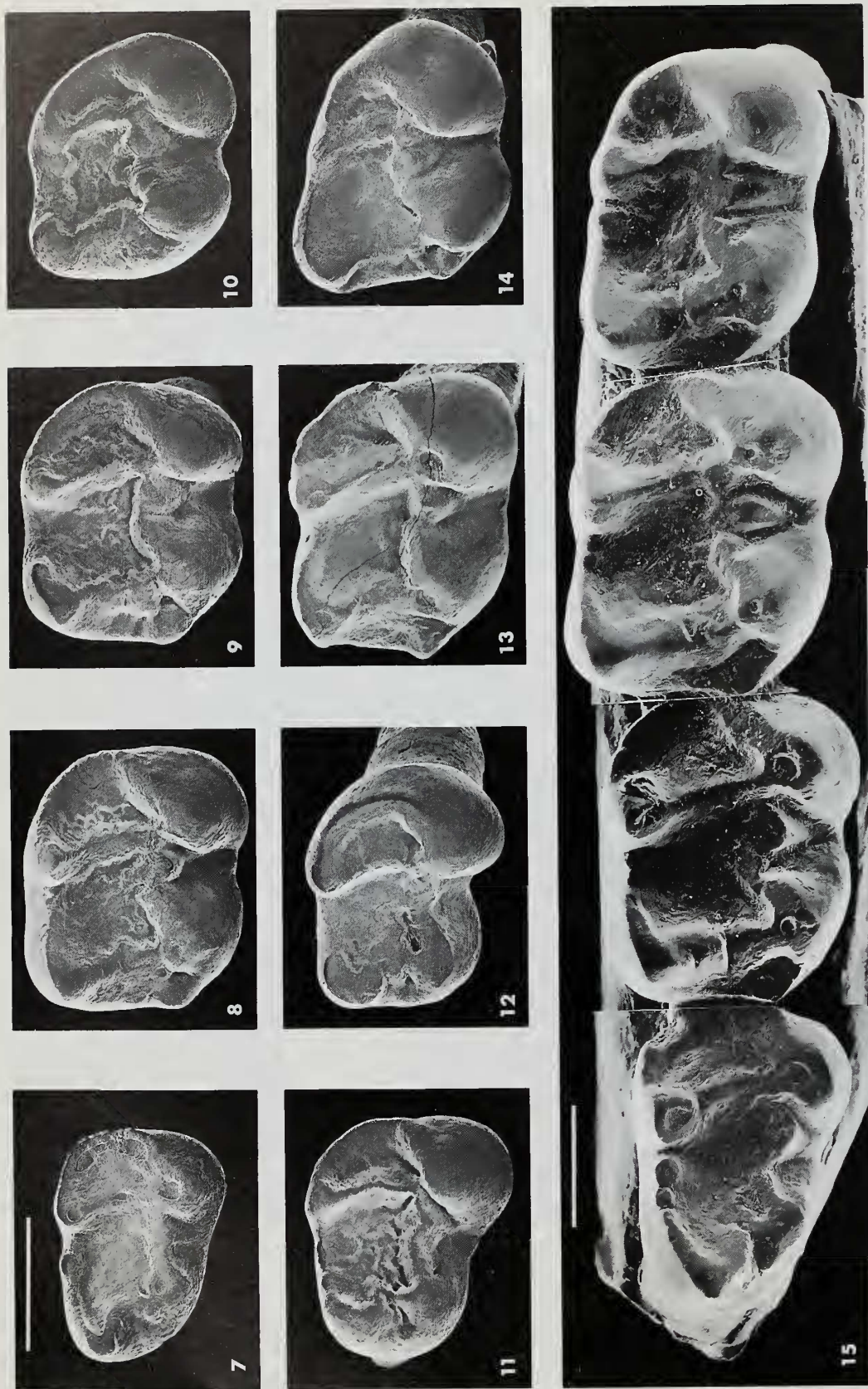
DIFFERENTIAL DIAGNOSIS. Other *Treposciurus* species are larger, tend to have densely wrinkled enamel and/or a lesser development of M¹⁻² metalophule 1 and have lower molars with stronger mesoconids and weaker anteroconids (see Schmidt-Kittler 1971; Bosma 1974; Hooker 1986).

DESCRIPTION. P₄, DP₄ and M_{1/2} tooth types are made known for the first time and contribute significantly to an understanding of the species and its distinction from *T. intermedius* (see p. 39). Variation in the separation of the protoconid and metaconid on the two P₄s can be seen in Figs 11-12. Complex variation in development of M¹⁻² metalophule 1 and of the coarse enamel folds in upper and lower molars can be seen in Figs 1-14 and Bosma (1974: pl. 6, figs 3-10). Other features such as strength of the lower cheek tooth mesoconid and anteroconid are remarkably constant, within the relatively small sample. The rounding of the buccal corners of upper molars is striking when present, but by no means constant. It is most marked in the specimens from WB2A (Bosma 1974: pl. 6, figs 6, 8-10). The outline shape of M₃ varies much (Figs 10, 14) in a similar way to that documented for *Treposciurus helveticus preecei* from the Bartonian of Creechbarrow (Hooker 1986: pl. 17, figs 4, 6), and reflects differing development of the entoconid and transverseness versus obliquity of the mesial margin. The length measurements of upper and lower preultimate molars have a low coefficient of variation (see Table 1). The holotype maxilla is broken a short distance anteriorly and medially of DP⁴ so the extent of the incisive foramen is unknown.

Other assemblages differ from the type assemblage slightly in size, but not in morphology (Table 1). The teeth from Fons 4 have mean lengths of M^{1/2} (1.62 mm) and M_{1/2} (1.65 mm) (Hartenberger 1973:16) slightly less than has the type assemblage of *T. gardneri*, with little overlap of measurements. Morphology clearly shows the Fons 4 assemblage is very

Table 1 Statistics of length and width measurements of cheek teeth of *Treposciurus*. (N = number of specimens; OR = observed range; \bar{x} = mean; s = standard deviation; v = coefficient of variation. Measurement in brackets is estimate). * = measurements taken from epoxy casts.

Sp./loc.	Tooth	Length					Width				
		N	OR	\bar{x}	s	v	N	OR	\bar{x}	s	v
<i>T. gardneri</i> Hordle Mammal Bed	DP ⁴	2	1.68-1.88	1.78			2	1.52-1.68	1.60		
	M ^{1/2}	8	1.66-1.80	1.77	0.048	2.70	8	1.61-2.04	1.82	0.143	7.85
	M ³	1		1.60			1		1.76		
	DP ₄	3	1.72-1.98	1.82			3	1.24-1.38	1.29		
	P ₄	2	1.76-1.80	1.78			2	1.44-1.54	1.49		
	M _{1/2}	10	1.76-1.96	1.88	0.065	3.42	10	1.50-1.72	1.63	0.066	4.09
	M ₃	4	1.86-2.02	1.94			3	1.52-1.66	1.58		
<hr/>											
<i>T. gardneri</i> above Cyrena cycladiformis Bed	M ^{1/2}	1		1.90			1		(1.96)		
<hr/>											
<i>T. gardneri</i> HH3-4	DP ⁴	1		1.92			1		1.66		
	*M ^{1/2}	1		1.65			1		1.64		
	*M ³	2	1.56-1.67	1.62			2	1.53-1.64	1.59		
	*M _{1/2}	2	1.74-1.86	1.80			2	1.45-1.56	1.51		
<hr/>											
<i>T. gardneri</i> Bembridge Limestone	M ^{1/2}	1		2.10			1		2.38		
	M _{1/2}	1		2.14			1		1.84		
<hr/>											
*Lectotype	DP ₄	1		2.48			1		1.80		
<i>T. intermedius</i>	M ₁	1		2.56			1		2.24		
Quercy	M ₂	1		2.72			1		2.26		
	M ₃	1		2.60			1		1.92		



Figs 7–15 SEMs of lower cheek teeth in occlusal view of *Treposciurus*, late Eocene. Figs 7–12, 14, paratypes of *Treposciurus gardneri* sp. nov., from the Mammal Bed, Hordle, Hants. Fig. 7, right DP₁ (reversed) (M44481); Fig. 8, right M_{1/2} (reversed) (M44487); Fig. 9, left M_{1/2} (reversed) (M44488); Fig. 10, left M₃ (M44496); Figs 11–12, left P₄s (M44484–5); Fig. 14, right M₃ (reversed) (M44497). Fig. 13, left M_{1/2} of *T. gardneri* sp. nov. from the Bembridge Limestone Formation, Headon Hill, Isle of Wight (M51104). Fig. 15, epoxy cast (coated with gold-palladium) of right DP₄, M_{1–3} of lectotype of *T. intermedium*, from the Phosphorites du Quercy, France (original BSPG.1879XV-192). Scale bars = 1 mm; original specimens uncoated.

closely related and, as Bosma (1974:53) noted, not a *Suevosciurus*, but the distinct plots of measurements leave doubt over precise conspecificity. The $M^{1/2}$ s from WB2A described by Bosma also lie outside the measurements of the type assemblage, being slightly larger. The small number of specimens (3) suggests that there would be overlap if more were known, but the single $M^{1/2}$ from the Bembridge Limestone is also slightly larger than any from the type assemblage. The Bembridge Limestone Formation and the Bembridge Marls Member of the Bouldnor Formation are demonstrably younger than the Mammal Bed at Hordle, by superposition, and Fons 4 is considered older, e.g. according to the evolutionary grade of its *Choeropotamus* (see Sudre 1978). It would therefore seem that there is a trend towards size increase, which could indicate that the Fons 4, Hordle and WB2 assemblages are segments of a single lineage. Curiously, however, the two upper molars from HH1 recorded by Bosma (1974) are also larger than any in the type assemblage. As the Mammal Bed and HH1 (only 8.5 km apart) both contain *Thalerimys headonensis*, they are penecontemporaneous (belonging to Bosma's 'Isotychus' headonensis Zone). Either none of the assemblages has yet been adequately sampled to show the size range, or a more complex pattern of size than a simple increase through time may pertain.

Discussion

Explanation of reidentification.

The type series of '*Sciuroides intermedius*' Schlosser, 1884 consisted of two dentaries and a maxilla from the old Quercy Phosphorites locality of Escamps, southern France. Dehm (1937) selected one of the dentaries as lectotype. Schmidt-Kittler (1970) erected the genus *Treposciurus* for *T. mutabilis* Schmidt-Kittler 1970 (type species) and for '*Sciuroides intermedius*' Schlosser 1884. Schmidt-Kittler (1971) removed the maxilla of the type series of *T. intermedius* from that species, because the posterior border of its incisive foramen reached back to P^4 in Schlosser's figure, thus contrasting with another Quercy maxilla figured by Thaler (1966), the dental match of which was better. Bosma (1974) claimed that the posterior border of the incisive foramen was damaged in the paralectotype maxilla and that the specimen could still belong in *T. intermedius*. Bosma was relying on referred maxillary specimens from Quercy for comparison with her Isle of Wight material, as her knowledge of the lower dentition was restricted to a single M_3 . She noted that these upper molars and the rather undiagnostic M_3 were morphologically similar to those of *T. intermedius*, but that they were slightly smaller. Whatever the true identity of the paralectotype maxilla, the lectotype dentary is all that one can rely upon for potential identification of other *T. intermedius* specimens. Inaccuracy of old Quercy locality names makes it impossible to recognize any unequivocal topotypes. Nevertheless, several upper dentitions from old Quercy collections appear to match adequately the lowers of the lectotype and other specimens; their distinguishing features have been tabulated by Schmidt-Kittler (1971: tab. 4). They include upper molars which differ strikingly from *T. gardneri* in having a symmetrical endoloph, coarsely wrinkled enamel and no metalophule I.

It can be seen that the teeth of the lectotype of *T.*

intermedius are significantly larger than the equivalents in *T. gardneri* (Figs 7–15). They have a stronger mesoconid and a higher length/width ratio. The M_{1-2} hypoconid encroaches further mesially on the sinusid and DP_4 and M_3 each have a prominent mesostylid. The last feature is variable in *T. gardneri*, occurring in one out of three DP_4 s and incipiently in one out of ten $M_{1/2}$ s; the others are constant for the available specimens.

What makes *T. gardneri* a *Treposciurus* and not a *Suevosciurus*? The recognition that the tooth types previously regarded as P_4^4 are in reality DP_4^4 (Hooker 1986) removes one distinction previously maintained. The most recently emended diagnoses of *Treposciurus* and *Suevosciurus* (Hooker 1986: 308, 315) do not polarize the characters, but a restriction to those in the advanced state is shown in Fig. 16. In *Suevosciurus*, upper and lower cheek teeth have basins that are deeper and more concave, the antero- and postero-lophs and lophids tend to be more prominent and the transverse lophs are more distinct; the upper molars tend to have an uninterrupted, more symmetrical endoloph, with any expression of metaconule 2 or metalophule I (which lack a dentine core) restricted to a lingual section; metalophule II joins the hypocone; M^3 shows more distal reduction with, in the contemporaneous species from Hordle, total absence of metalophule II, a much shallower sinus and more mesially positioned protocone (compare the present figures with Bosma 1974: pl. 6, fig. 10). The lower molars usually lack an anterolophulid and have a stronger mesoconid which, in the contemporaneous species from Hordle (amongst others), is usually linked by a crest to the mesiobuccal corner of the hypoconid (Figs 22–23); and DP^4 usually has a concave mesiolingual margin (Figs 17–18).

Evidence for a late Eocene speciation event.

Hooker (1986) formulated a model of cladogenetic speciation in the genus *Treposciurus*. He envisaged a morphologically very variable *T. helveticus* of the Bartonian giving rise around the Bartonian–Ludian boundary to *T. intermedius* and *T. mutabilis* by respective selection of two morphs present together in the ancestral species and by size differentiation. He divided *T. helveticus* (raised to species level from *T. mutabilis helveticus* Schmidt-Kittler 1971) into two subspecies: a nominate one from Eclépens B, Switzerland, and *T. h. preecei* from Creechbarrow. Current detailed study of the Eclépens B material (Hooker & Weidmann, in prep.) shows that *T. h. helveticus* involves greater complexity. The Eclépens B *Treposciurus* is therefore simply referred to as *Treposciurus helveticus* Schmidt-Kittler 1971, and the subspecies *T. helveticus preecei* Hooker 1986 is hereby raised to species level as *Treposciurus preecei* Hooker 1986 new rank.

These nomenclatural changes do not affect the evidence for the speciation event, but they do mean that the ancestral species is now *T. preecei*, and one daughter species is *T. gardneri*, whilst the other daughter branch is at present an unresolved complex comprising *T. mutabilis*, *T. helveticus* and *T. intermedius*. The evidence based on character analysis is presented in Fig. 16. Here a cladogram shows the splitting of *Treposciurus gardneri* from the rest and also the characters linking the genus *Treposciurus* to its nearest sister taxon *Suevosciurus*. Character polarity was obtained by outgroup comparison with the rest of the Pseudosciuridae.

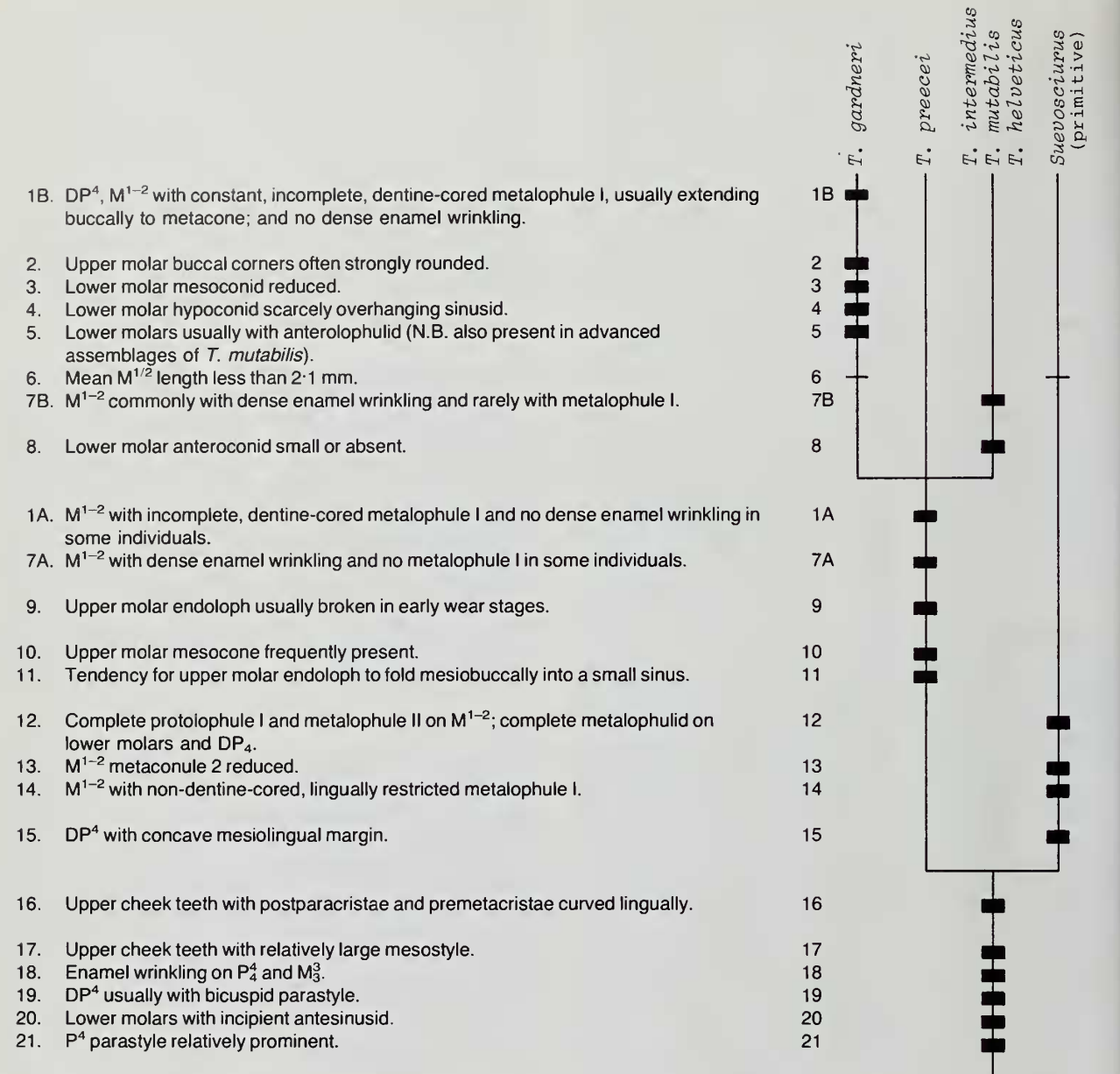
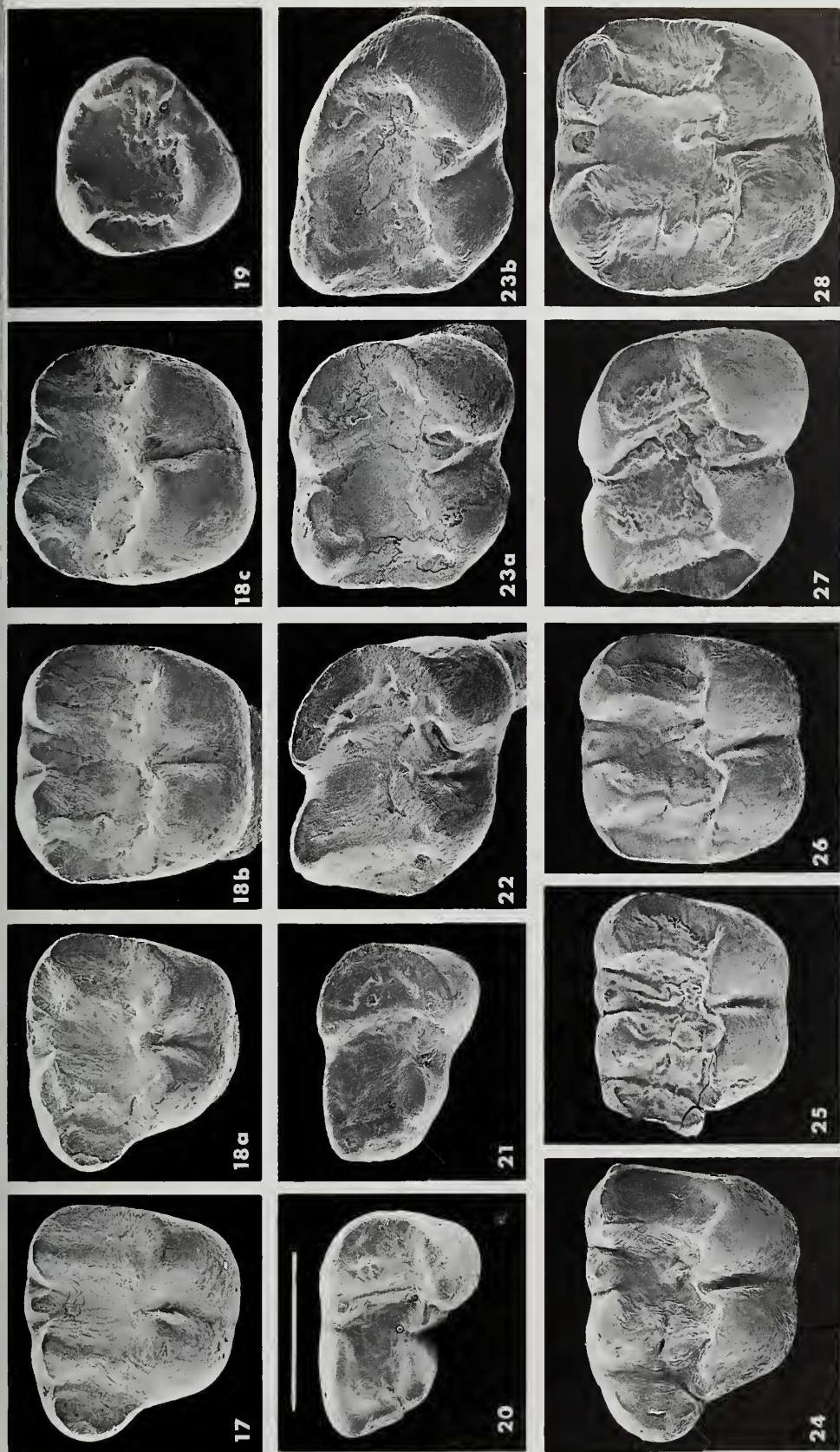


Fig. 16 Cladogram of species of *Treposciurus* and the genus *Suevosciurus*. Synapomorphies indicated by broad bar, parallelisms by narrow bar. Characters 1 and 7 are multistate.

Genus SUEVOSCIURUS Dehm 1937		v. 1987	<i>Suevosciurus</i> sp. 1; Collinson & Hooker: 292.
		v. 1987	<i>Suevosciurus</i> sp. nov.; Hooker: 112.
TYPE SPECIES. <i>Sciurioides fraasi</i> Major 1873.		v. 1989	<i>Suevosciurus</i> sp. nov.; Hooker: fig. 2.
<i>Suevosciurus bosmae</i> sp. nov. Figs 17–23, 30E, F			
vp. 1974	<i>Suevosciurus palustris</i> (Misonne 1957); Bosma: 34–44; pl. 5, figs 7–9.		
v. 1980	<i>Suevosciurus palustris</i> (Misonne 1957); Hooker & Insole: 39.		
vp. 1982	<i>Suevosciurus palustris</i> (Misonne 1957); Russell <i>et al.</i> : 57.		
v. 1986	<i>Suevosciurus</i> ; Hooker: 322–327.		
		HOLOTYPE. Right DP ⁴ –M ² (M51095) (Fig. 18). This specimen is chosen because it shows associated cheek teeth of one individual. Although found isolated, they were from the same sample and their matching interstitial facets demonstrate association. A left DP ⁴ of identical morphology, size and wear state to the holotype DP ⁴ is probably also associated (Fig. 17), but as a conservative approach it is listed as a paratype.	



Figs 17–28 SEMs of cheek teeth in occlusal view of *Suevosciurus*, Solent Group, late Eocene, Isle of Wight. Figs 17–23, *S. bosmae* sp. nov., from green clay below How Ledge Limestone, Headon Hill. Fig. 18, holotype, associated right DP⁴ (a), M¹ (b), M² (c) (reversed) (M51095). Figs 17, 19–23 are paratypes; Fig. 17, left DP⁴ (M51096); Fig. 19, epoxy cast of left M¹ (original GIU.941); Fig. 20, epoxy cast of right DP⁴ (reversed) (original GIU.816); Fig. 21, epoxy cast of left DP⁴ (original GIU.815); Fig. 22, left M^{1/2} (M51098); Fig. 23, associated right M² (A) and M³ (B) (reversed) (M51097). Figs 24–27, *S. fraasi*, from the Bembridge Limestone Formation, Headon Hill. Figs 24–25, left DP⁴s (M51090–1; the latter's parastyle is slightly broken); Fig. 26, left M^{1/2} (M51093); Fig. 27, left M^{1/2} (M51094). Fig. 28, left M^{1/2} (M49489) of *S. ehingenensis*, from the Bembridge Limestone Formation, Headon Hill. Scale bar = 1 mm; casts are coated with gold or gold palladium, originals are uncoated.

PARATYPES. Left DP⁴ (M51096) (Fig. 17); left M³ (GIU941) (Fig. 19); right DP₄ (GIU816) (Fig. 20); left DP₄ (GIU815) (Fig. 21); left M_{1/2} (M51098) (Fig. 22); right M₂₋₃ (M51097) (Fig. 23).

NAME. For Dr Anneke Bosma, Utrecht, in recognition of her work on fossil rodents.

TYPE HORIZON AND LOCALITY. Green clay below the How Ledge Limestone (includes Bosma's (1974) sample locality HH2) near top of Totland Bay Member, Headon Hill Formation, SW Headon Hill, Isle of Wight.

REFERRED MATERIAL. Topotype isolated teeth M33371, M51096 and M51098–51102. Also Bosma's (1974) material in the GIU from the Totland Bay Member of Headon Hill (HH1, 2) (topotypes) and Totland Bay; and Lignite Bed in Hatherwood Limestone Member of Headon Hill (HH3, 4, B and C) (except GIU 426, 480, 492 and 499 which belong to *Treposciurus gardneri*). Additional isolated teeth from shelly lenses at base of lignite bed (same level as HH3 of Bosma 1974) (M51106–51129).

DIAGNOSIS. Mean length of M^{1/2} = 1.55 mm; range 1.39–1.67 mm. P₄⁴ absent. DP⁴ mean length/width ratio 1.17–1.19. M³ without distinct metalophule II and often with weak paraconule. DP⁴ with width at paracone and protocone less than width at metacone and hypocone; no lingual parastylar notch. Lower molars nearly always with crest joining mesoconid to hypoconid.

DESCRIPTION. Much of the morphological variation has been described qualitatively by Bosma (1974). An attempt has been made in Tables 2–3 to quantify this to provide a means of comparison with *Suevosciurus authodon* from the Bartonian of Creechbarrow (Hooker 1986). Dividing lines between categories are admittedly often arbitrary and can often be documented only in relatively little-worn teeth, but despite these shortcomings this methodology can still demonstrate broad trends and differences. Only the assemblages from the green clay below the How Ledge Limestone (including HH2) near the top of the Totland Bay Member, and the shelly lenses at the base of the lignite bed in the Hatherwood Limestone (including HH3) were considered large enough for this quantitative treatment, and neither are as large as that from Creechbarrow.

Table 2 Percentage character analysis of upper cheek teeth of *Suevosciurus bosmae* from the green clay below How Ledge Limestone (HH2) and from shelly lenses at base of Lignite Bed (HH3). 'Scoring units' give states for characters described in the left-hand column. The numbers given under the tooth-headed columns on the right are percentages and refer to the number of teeth showing that particular character state. The final lines of figures in brackets in the left-hand column are the respective numbers of each tooth type represented. See Hooker (1986:296, text-fig. 31) for relevant dental nomenclature diagram.

Characters + (N) of respective teeth	Scoring units	DP ⁴		M ¹⁻²		M ³	
		HH2	HH3	HH2	HH3	HH2	HH3
Metalophule I shape: metaconule 1 only (1), ridge (2) (8) (5) (16) (8)	1	12	0	6	25		
	2	88	100	94	75		
Metalophule I joins endoloph (1), hypocone (2), metalophule II (3), endoloph and hypocone (4), hypocone and metalophule II (5), endoloph and metalophule II (6), all three (7), none (0) (8) (6) (13) (9)	0	12.5	0	7.5	22		
	1	37.5	33.2	62.0	78		
	2	37.5	16.7	23.0	0		
	3	0	16.7	0	0		
	4	0	0	0	0		
	5	0	16.7	0	0		
	6	12.5	16.7	7.5	0		
	7	0	0	0	0		
Metalophule II broken/unbroken (14) (9) (31) (22) (15) (9)	B	14	0	16	36	100	0
	U	86	100	84	64	0	0
Enamel wrinkling (0–3) (13) (9) (23) (16) (11) (10)	0	46	11	0	6	0	0
	1	23	56	56	50	9	10
	2	23	33	35	31	73	80
	3	8	0	9	13	18	10
Mesostyle size (0–4) (16) (9) (37) (23) (16) (11)	0	0	0	0	0	6	27
	1	19	0	16	22	0	0
	2	56	67	70	56	0	18
	3	19	33	14	22	44	9
	4	6	0	0	0	50	46
Mesostyle saliency: prominent (3), slight (2), non- (1), ectoflexus (0) (15) (9) (33) (20) (16) (9)	0	0	22.0	18	20	0	0
	1	20	33.5	70	55	6	33
	2	67	33.5	12	25	69	67
	3	13	11.0	0	0	25	0

Table 2 (contd)

Characters + (N) of respective teeth	Scoring units	DP ⁴		M ¹⁻²		M ³	
		HH2	HH3	HH2	HH3	HH2	HH3
Mesoloph length (0-2) (14) (9) (32) (21) (15) (11)	0	7	0	16	33	100	100
	1	57	89	75	43	0	0
	2	36	11	9	24	0	0
Protolophule I broken/unbroken (11) (8) (35) (19) (8) (9)	B	0	0	6	11	25	89
	U	100	100	94	89	75	11
Metaconule 2 absence/presence (16) (9) (38) (23)	0	50	89	79	78		
	1	50	11	21	22		
Hypolophule absent (0), partial (1), complete (2) (13) (9) (35) (20)	0	85	78	77.0	75		
	1	15	22	11.5	15		
	2	0	0	11.5	10		
Posteroloph broken/unbroken lingually (7) (9) (22) (18)	B	0	11	23	17		
	U	100	89	77	83		
Mesocone absence/presence (15) (9) (38) (21) (16) (11)	0	100	100	100	100	87.5	100
	1	0	0	0	0	12.5	0
Sinus depth: shallow (1) to deep (4) (17) (9) (38) (21) (15) (11)	1	0	0	0	0	60	45.5
	2	12	67	10	5	40	45.5
	3	70	22	82	81	0	0
	4	18	11	8	14	0	9
Protostyle absence/presence (16) (8) (38) (21) (15) (10)	0	75	37.5	89	76	100	90
	1	25	62.5	11	24	0	10
Hypostyle absence/presence (9) (8) (25) (4)	0	78	100	52	50		
	1	22	0	48	50		
Paraconule absent (0), small (1), large (2) (16) (9) (37) (23) (13) (10)	0	0	0	0	0	0	10
	1	6	0	3	13	62	70
	2	94	100	97	87	38	20
Endoloph broken (1), complete (2) (8) (9) (21) (17) (7) (11)	1	0	11	0	12	0	18
	2	100	89	100	88	100	82
DP ⁴ parastyle bicuspid (9) (8)	0	44	37.5				
	1	56	62.5				
DP ⁴ mesiolingual margin concave (16) (8)	0	6	37.5				
	1	94	62.5				

Because of the small sample numbers, first and second molars were not distinguished. Many of the characters show a distribution similar to that in *S. authodon*. However, there is a general tendency in a number of the characters for one morphology in the range to dominate more than in *S. authodon*. In other words there is a slight reduction in variation. M³ shows the greatest number of differences. Its distal reduction compared to *S. authodon* means that most specimens have lost their mesoloph and metalophule II (and, in the few that retain it, it is discontinuous), and reduced the depth of the sinus, the incidence of a protostyle, and the size of the paraconule. Mesiodistal elongation of the mesostyle is

restricted to M³, having been lost from the other upper cheek teeth. In both upper and lower cheek teeth there is an increase in enamel wrinkling intensity on DP⁴-M². In the lower molars the hypoconulid present in some M_{1/2}s of *S. authodon* is not encountered in the *S. bosmae* assemblages. There is also a reduction in the incidence of the distal crest to the hypolophulid. There is a slight shift in the average position of attachment of the ectolophid to the hypolophulid in M₃, so that in a greater proportion the attachment is at or very close to the hypoconid. The biggest difference is in the increase in the proportion of teeth where the mesoconid is linked to the buccal side of the hypoconid by a crest, thus

Table 3 Percentage character analysis of lower cheek teeth of *Suevosciurus bosmae* from HH2 and HH3, as in Table 2.

Characters + (N) of respective teeth	Scoring units	DP ₄		M ₁₋₂		M ₃	
		HH2	HH3	HH2	HH3	HH2	HH3
Distance along hypolophulid from hypoconid of junction with ectolophid (7) (6) (20) (20) (9) (12)	<¼	71	83	65	80	100	83
	¼	29	0	35	20	0	17
	no link	0	17	0	0	0	0
Anteroconid size (22) (18) (9) (12)	1			27	17	0	33
	2			32	44	89	67
	3			36	39	11	0
	4			5	0	0	0
Anterolophulid absent (0), weak (1) (20) (16) (6) (12)	0			85	62.5	100	42
	1			15	37.5	0	58
Mesoconid with crest linking buccally with hypoconid (10) (6) (24) (21) (9) (12)	0	50	83	21	19	0	0
	1	50	17	79	81	100	100
Enamel wrinkling (0-3) (6) (6) (14) (16) (7) (10)	0	0	0	0	0	0	0
	1	50	100	43	44	29	20
	2	33	0	43	50	71	60
	3	17	0	14	6	0	20
Mesostylid absence/presence (10) (6) (23) (21) (9) (12)	0	100	83	96	81	44	92
	1	0	17	4	19	56	8
Ectostylid absence/presence (10) (6) (24) (21) (9) (12)	0	100	100	100	95	100	100
	1	0	0	0	5	0	0
Hypoconulid absence/presence (8) (6) (16) (17) (6) (11)	0	100	100	100	100	100	100
	1	0	0	0	0	0	0
Distal crest to hypolophulid absence/presence (8) (6) (16) (18) (6) (11)	0	100	100	100	94	100	64
	1	0	0	0	6	0	36

isolating the distal part of the sinusid as a discrete fossa. The change is most marked in M₃, least marked in DP₄. Linkage makes it impossible to allocate mesoconid length categories (cf. Hooker 1986).

None of the morphological differences between these two assemblages of *S. bosmae* appears significant. A possible exception is the M³ protolophule I, which shows a dominantly broken or interrupted state in the Hatherwood Limestone (HH3) assemblage, in contrast to both the How Ledge Limestone (HH2) and Creechbarrow assemblages, but in common with those of later *S. fraasi* (Schmidt-Kittler 1971:42).

Discussion

Distinction of S. bosmae from other small Suevosciurus. Hooker (1986:327) proposed that 'teeth from the Headon Beds (referred by Bosma 1974 to *S. palustris*)' should be placed in a new species, but did not name it (herein named *S. bosmae*). He explained that the assemblages in question have upper cheek teeth with a constantly larger mesostyle, whereas in all those of true *S. palustris* (admittedly few and restricted

to the type assemblage from Hoogbutsel) the mesostyle is either very small or absent. Moreover, the only two known lower molars of *S. palustris* (both IRSNB.IG18061) have a mesoconid that is not joined by a crest to the mesiobuccal corner of the hypoconid. Common occurrence of this state is shared with *S. minimus* (Schmidt-Kittler 1971: 48; pl. 2, fig. 5) and *S. authodon* (Hooker 1986: 321). Most lower cheek teeth of *S. bosmae* have the crest joining mesoconid to hypoconid, in common with assemblages of *S. fraasi* and *S. ehingensis* from southern Germany (Schmidt-Kittler 1971: 42-47). Interestingly, they are also paralleled by some individuals of *Treposciurus m. mutabilis* (Schmidt-Kittler 1971: 53, fig. 22i).

It is relatively simple to distinguish *S. bosmae* from similarly-sized *S. palustris*, but less so from other assemblages of small *Suevosciurus*. Hooker (1986: 325), using mainly published measurements, combined data from the Hampshire Basin and Bavaria (southern Germany) to produce a phylogenetic pattern of change in *Suevosciurus* assemblages through time. It essentially followed the concept of Schmidt-Kittler (1971) of two evolving lineages in the latest Eocene and Oligocene of southern Germany, except that it removed *S.*

minimus from a common ancestral position, replacing it with the taxon here named *S. bosmae*. An unsolved problem over the two lineage model of Schmidt-Kittler was the near total reliance on size for distinguishing each lineage, which itself undergoes size increase with time. On this basis, therefore, one cannot identify certain of the assemblages without recourse to knowledge of their age. Bosma (1974: 41–43) thus resorted to an arbitrary division of species on size, which could be considered more parsimonious in the absence of other morphological evidence. Hooker (1986: 326–327) found a gradual increase in length/width proportions of DP⁴, through at least the lower part of the sequence, which served to distinguish further some of the similarly-sized assemblages, although problems remained in the probable region of differentiation of *S. fraasi* and *S. ehingensis*.

One of the assemblages which Schmidt-Kittler (1971) placed in *S. fraasi* and Bosma (1974) placed in *S. palustris* is from Ehrenstein 1. This fissure filling contains faunas of two different ages, labelled A and B, so intermixed that they can only be distinguished by comparing each element with those in stratified deposits of known age (Schmidt-Kittler 1969, 1971). The later fauna (B) dates from just after the Grande Coupure, the earlier (A) from the middle of the late Eocene, approximately the age of the Lacey's Farm Limestone Member, Headon Hill Formation of the Isle of Wight. Schmidt-Kittler (1971) considered that of the three *Suevosciurus* species, *S. minimus*, the most primitive, came from the A fauna, whereas *S. fraasi* and *S. ehingensis* came from the B fauna. This means that from just pre-Grande Coupure time (Bernloch 1A/Weissenberg 2) onwards, the otherwise constantly sized *S. fraasi* lineage underwent a rapid size decrease (Ehrenstein 1B) followed by similar increase soon afterwards (Ehingen 12) (see Hooker 1986: text-fig. 38). Schmidt-Kittler (1971: 47) noted some minor morphological differences between his *S. fraasi* and *S. ehingensis* lineages: slightly blunter and more voluminous main cusps and somewhat weaker parastyle on DP⁴ in the latter. In fact there is a tendency for DP⁴s of post-Grande Coupure assemblages of *S. fraasi* to be dominated by the two morphs that Schmidt-Kittler (1971: 42) described: linguallally displaced parastyle, causing a very oblique buccal parastyle margin (his fig. 16b); and notch in the mesial outline just lingual to the parastyle (his fig. 16d). In *S. ehingensis* these morphs are either rare or less clearly developed. The pre-Grande Coupure assemblages referred to *S. fraasi* are less distinct but in common with the post-Grande Coupure ones tend to have the widths of DP⁴ across paracone–protocone and metacone–hypocone approximately equal. In *S. ehingensis* the mesial width tends to be slightly shorter than the distal width, in common with *S. bosmae* and *S. authodon* (Fig. 30). DP⁴s referred to *S. fraasi* in the Ehrenstein 1 assemblage are morphologically less distinct than the other post-Grande Coupure assemblages and, together with their small size, would thus fit better in the Ehrenstein 1A than the 1B fauna.

Recently, Heissig (1987) has described a new small species of *Suevosciurus*, *S. dehmi*, from the immediately post-Grande Coupure Bavarian fissure filling of Mohren 31. The type assemblage is slightly larger than *S. bosmae* but overlaps slightly with it. It could weaken the evidence for the timing of the speciation event envisaged here by potentially supporting the B age for Ehrenstein 1 *S. fraasi* (the intermediate-sized species), through the latter's possible identification as *S. dehmi*. It does not, however, disprove it. Heissig (1987:102, fig. 1) did not include the plot of the intermediate-sized

Suevosciurus from Ehrenstein 1, but, from Schmidt-Kittler's (1971) text-fig. 20, it would superimpose the type assemblage of *S. dehmi*. Unfortunately, Heissig did not diagnose *S. dehmi* on characters other than size and it is thus difficult to fit it into a scheme based on morphology. However, his figure (Heissig 1987: pl. 1) of the holotype right dentary with DP₄ (not P₄), M₂ and M₃ shows the molar mesoconids joining the hypoconids as is usual for *S. fraasi*, *S. ehingensis* and *S. bosmae*. If the intermediate-sized *Suevosciurus* from Ehrenstein 1 is indeed *S. dehmi*, then its relationships appear closer to *S. fraasi* than to *S. ehingensis*, perhaps introducing paraphyly for *S. fraasi*. However, decision must await publication of morphological details of *S. dehmi*.

Evidence for a late Eocene speciation event.

To clarify ideas of relationships of the advanced species of *Suevosciurus* (i.e. those that have lost P₄), a cladistic analysis is presented here, using the admittedly variable morphological differences in addition to size. *S. authodon* is used as out-group to polarize the characters. The placement of *S. palustris* is doubtful, as neither DP₄ nor P₄ tooth types are known, and assumes that characters 7 and 8 are in the advanced state (Fig. 29).

If the Ehrenstein 1 assemblage referred to *S. fraasi* is from the A fauna, as advocated above, it is envisaged that initial differentiation of *S. fraasi* and *S. ehingensis* from the probable ancestral species *S. bosmae* took place, in the former by protocone expansion causing mesial broadening with incipient lingual parastyle notching of DP⁴ but with little size increase, and in the latter simply by a greater increase in size unaccompanied by DP⁴ shape changes (Figs 30, 31). According to this model the most primitive *S. fraasi* assemblage would be that of Ehrenstein 1, whereas the most primitive *S. ehingensis* assemblage would be that of Lacey's Farm Quarry (Lacey's Farm Limestone Member) (identified on size as *S. fraasi* by Bosma & Insole 1976). There seems also to be a slight size increase of DP⁴ over the molars in *S. fraasi*, so that DP⁴s from Ehrenstein 1 are about the same size as those from Lacey's Farm Quarry, whereas the molars of the former are smaller; by the time of Weissenburg 8, *S. ehingensis* DP⁴s had enlarged proportionally also (Fig. 30). Subsequent patterns of change, in addition to size increase in both lineages (causing advanced assemblages of *S. fraasi* to have character 3), involve repeated elongations and shortenings of DP⁴ (Hooker 1986: text-fig. 39), as well as subtle shape changes. None of these, however, affects recognition of the diagnostic *S. fraasi* DP⁴s provided assemblages are large enough. These changes thus comprise variation within a lineage which could be discriminated taxonomically at the level of stratigraphical subspecies (e.g. as Franzen, 1968, has done for *Palaeotherium*).

In further support of the speciation model, rare specimens of both *S. fraasi* and *S. ehingensis* have been found in the argillaceous beds of the Bembridge Limestone Formation of Headon Hill (= HH6–7 of Bosma, 1974). *S. ehingensis* is represented by three M^{1/2}s slightly larger than those from Lacey's Farm Quarry, whilst *S. fraasi* is represented by three DP⁴s, one M^{1/2} and one M_{1/2} (Figs 24–28). The teeth of *S. fraasi* are all significantly smaller than the equivalent tooth types from Lacey's Farm Quarry; moreover, the DP⁴s have a greater length/width ratio, equal widths at both paracone–protocone and metacone–hypocone, and larger, more prominent parastyle with lingual notch.

The highest definite record of *S. bosmae* is from HH4. A few teeth from higher up in marly beds at the top of the

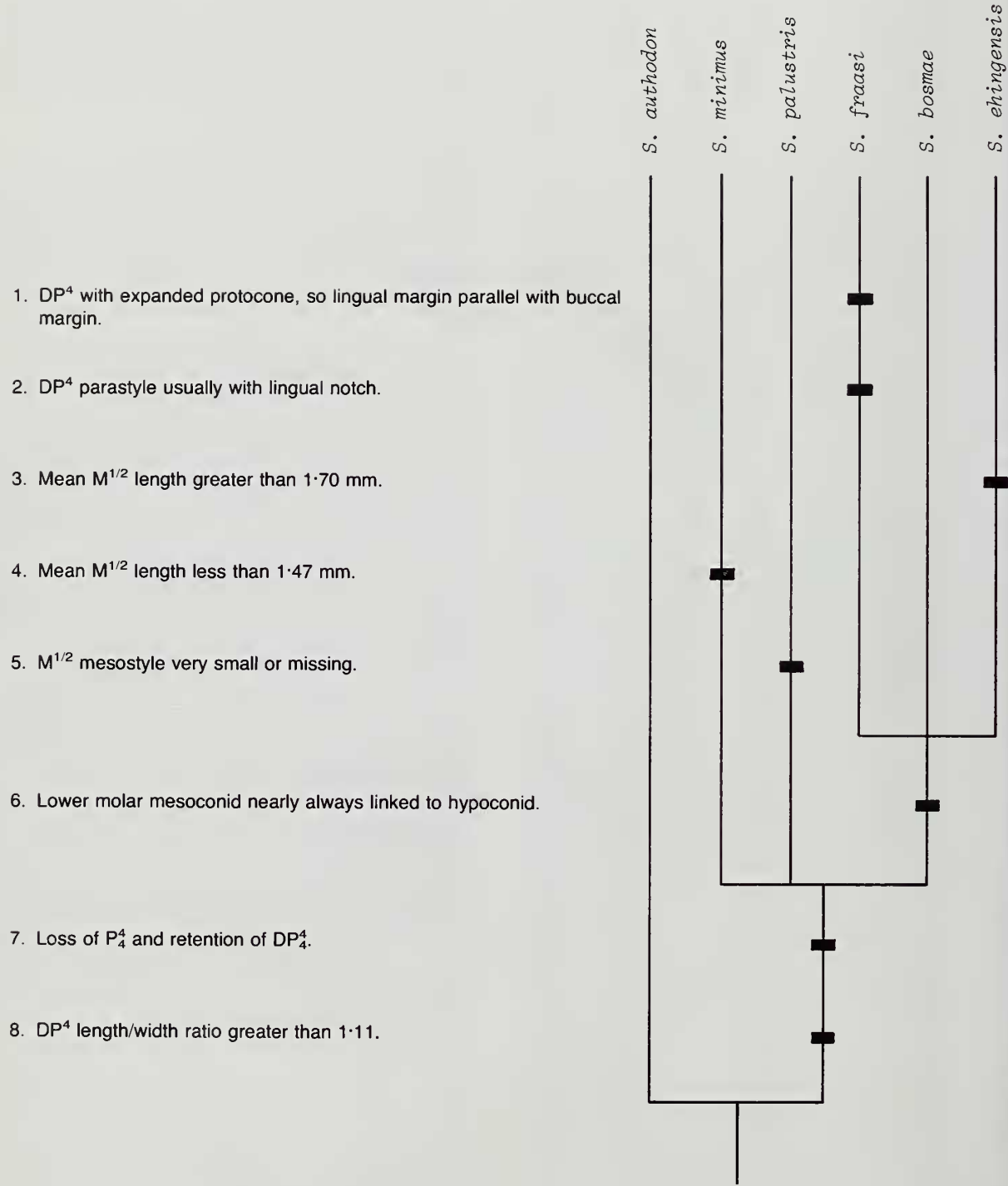


Fig. 29 Cladogram of species of *Suevosciurus*. Synapomorphies and autapomorphies are indicated by broad bar. See Fig. 16 for synapomorphies of the genus.

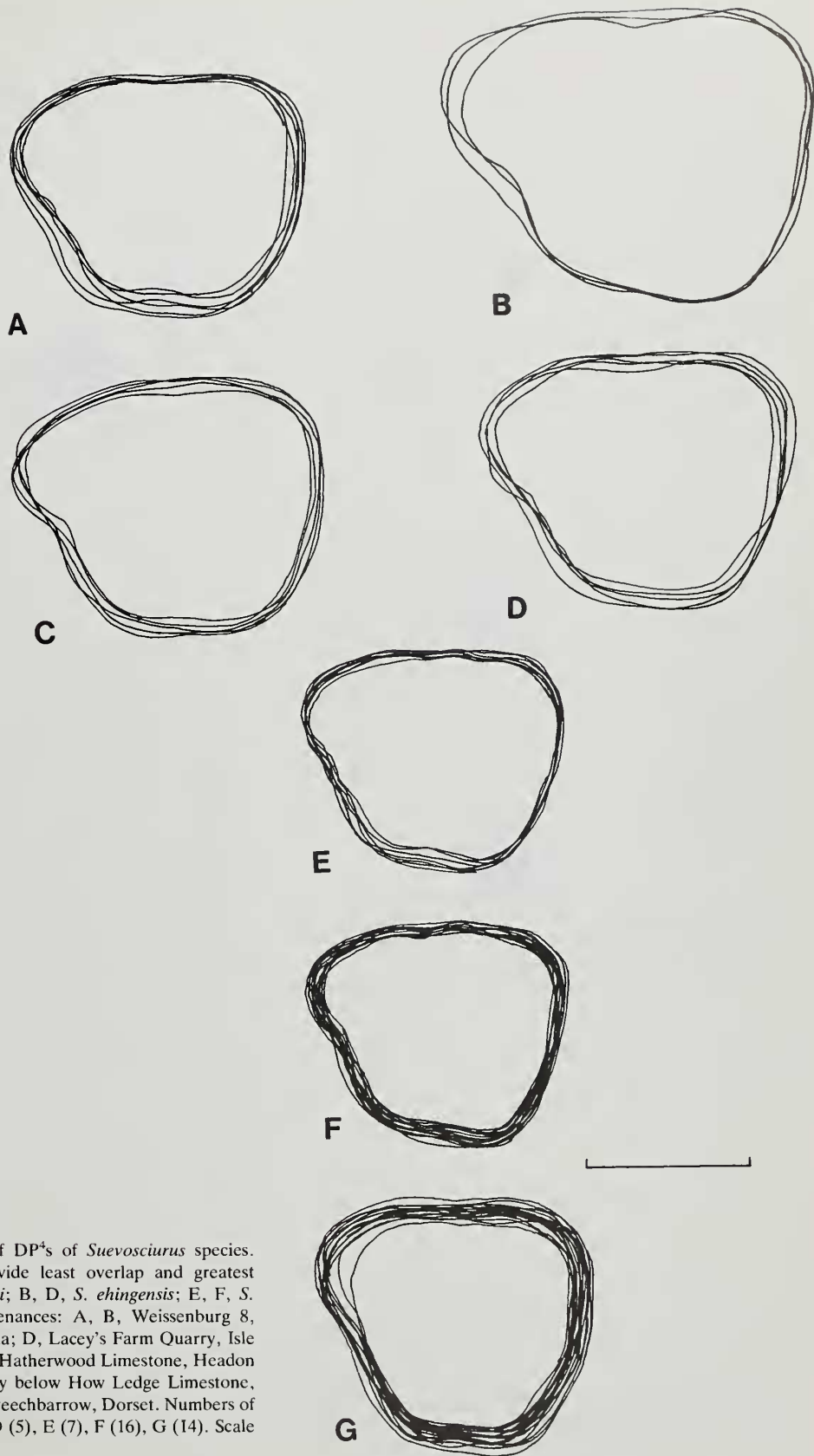


Fig. 30 Superimposed outlines of DP⁴s of *Suevosciurus* species. Superimposed manually to provide least overlap and greatest shape alignment. A, C, *S. fraasi*; B, D, *S. ehingensis*; E, F, *S. bosmae*; G, *S. authodon*. Provenances: A, B, Weissenburg 8, Bavaria; C, Ehrenstein I, Bavaria; D, Lacey's Farm Quarry, Isle of Wight; E, base of lignite bed, Hatherwood Limestone, Headon Hill, Isle of Wight; F, green clay below How Ledge Limestone, Headon Hill, Isle of Wight; G, Creechbarrow, Dorset. Numbers of specimens: A (6), B (3), C (5), D (5), E (7), F (16), G (14). Scale bar = 1 mm.

Hatherwood Limestone Member of slightly larger mean size (Fig. 31) may represent *S. bosmae*, but the sample as yet lacks the distinctive DP⁴. The next record of a *Suevosciurus* is of *S. ehingensis* from the Lacey's Farm Limestone Member, penecontemporaneous with the earliest record of *S. fraasi* at Ehrenstein 1. The evidence available suggests that the speciation event took place within the time represented by deposition of the intervening Cliff End Member at Headon Hill and may have resulted from isolation of populations in the southern English and Bavarian areas respectively. At some time after the deposition of the Lacey's Farm Limestone, and before deposition of the Bembridge Limestone, renewed dispersal to both areas became possible. Species distribution patterns in other genera of mammals from this sequence do not point to other contemporaneous speciation events, although from at least this time until well into the Oligocene, Bavaria had largely endemic faunas (Schmidt-Kittler & Vianey-Liaud 1975; Heissig 1978), and the earlier northern European region as portrayed by Franzen (1968) was split into two by Schmidt-Kittler & Vianey-Liaud (1975), with the boundary at the Rhine Graben. Ziegler (1982) records the Rhine Graben as a site of vulcanism and marine transgression in the late Eocene, which may well have been the isolating mechanism for the *Suevosciurus* speciation. If so, however, it did not prevent the newly formed species from migrating subsequently in both directions.

Speciation patterns

Cladogenetic speciation events have been recorded for several groups of mammals in the dense early Eocene record of the Bighorn Basin, Wyoming, U.S.A., in addition to the more obvious anagenetic events (e.g. Gingerich 1974, 1976, 1977, 1980; Gingerich & Simons 1977). In most cases, however, as one traces two lineages back in time, it is possible to follow only one of them right to an ancestral species, although the pattern of change implies derivation of both from a common ancestor (e.g. Gingerich 1976). A similar pattern has also been described for European Eocene primates (Godinot 1985). At first described as parapatric, this type of cladogenetic speciation was later considered to be allopatric, but where most of the morphological differentiation took place subsequently anagenetically and sympatrically (Gingerich 1977: 491–493). An important problem, however, remains: the lack of similarly dense fossil sequences in areas outside the Bighorn Basin, where the missing branch segment might be represented. Although the late Eocene/early Oligocene mammalian record in Europe is not as dense as in the early Eocene of the Bighorn Basin, and although the sequence in Bavaria is based on biostratigraphy of other mammals, not on superposition, a roughly equal resolution of mammalian faunal succession is recognizable in two European areas. Moreover, in each, it is possible to trace the two lineages of *S. fraasi* and *S. ehingensis* back in time until the former appears in southern England and the latter appears in southern Germany. Earlier than this in the late Eocene of southern England, only a single species (*S. bosmae*) occurs, which is primitive with respect to both *S. fraasi* and *S. ehingensis*. The pattern envisaged here is consistent with a more traditional idea of allopatric speciation, where geographic isolation results in morphologic as well as genetic differentiation before remixing of populations (the 'dumbbell' model – White 1978; Mayr 1982). It may simply have happened that isolation time lasted longer here. Alternatively, smaller population sizes in Eocene 'island' Europe

may have produced more rapid character changes. For instance, geographical ranges of some of the critical Bighorn Basin mammals seem to have been large, extending at least from Wyoming to New Mexico (e.g. Gingerich & Simons 1977). The distance between the two European areas under consideration is about 900 km and the maximum area potentially involved (i.e. delimited to the south by a line drawn from Paris to Geneva, as *Suevosciurus* only occurs very rarely further south), judged from palaeogeographic reconstructions (e.g. compilations by Ziegler 1982 and Hooker 1986) is about 300,000 km². This is no bigger than the state of Wyoming alone.

It is interesting to note that the newly discovered specimens of *S. fraasi* and *S. ehingensis* in the Bembridge Limestone tend to occur at different levels. Moreover, the former is associated with other taxa, such as primates, an apatemyid and a bat, all small forms which suggest a forested environment. In contrast, the latter is associated with other taxa such as the ungulates *Plagiolophus* and *Diplobune*, which suggest a slightly more open environment. This may indicate habitat differences which were directly related to their speciation. Taphonomic study of this sequence in progress may shed further light on this matter.

There are various potential tests for this speciation event. For instance, to find an Ehrenstein 1 stage *S. fraasi* in a Bavarian fissure containing a single-aged fauna would determine which of the two possible ages was right. The undescribed material from Ehrenstein 2, 3 and 6, Herrlingen 3 and Arnegg 3, listed as '*Suevosciurus minimus* – *fraasi* (Übergangsform)' by Schmidt-Kittler (1977) could provide the answer. Moreover, the finding of even earlier fissures in this area containing *S. bosmae* would support the isolation model. Conversely, the finding of *S. fraasi* in the Lacey's Farm Limestone Member or contemporaneous strata in the Isle of Wight, or of *S. ehingensis* in a fissure filling the same age as the Ehrenstein 1A fauna in Bavaria, would suggest that the speciation pattern was instead like that documented in the Bighorn Basin for, e.g., *Hyopsodus* and *Cantius* (Gingerich 1977).

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